

SYSTEMATICS OF *MALACOTHRIX PHAEOCARPA*, A NEW
SPECIES RELATED TO *M. FLOCCIFERA*
(ASTERACEAE: LACTUCEAE)

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ABSTRACT

Malacothrix phaeocarpa, new species from the California Floristic Province, is described. The new species is self-compatible and self-pollinating, and closely resembles the self-incompatible species *M. floccifera* from which it differs chromosomally and in several floral features.

During a study of herbarium specimens of *Malacothrix floccifera* (DC.) S. F. Blake a number of atypical specimens were found that were very similar to *M. floccifera* in vegetative features but different in several floral features. Chromosome associations in meiosis in hybrids, produced in cultivation between representatives of three populations of these plants and representatives of four populations of *M. floccifera*, indicate that there are also chromosomal differences. In this paper a new species, *M. phaeocarpa*, will be described, and evidence concerning its relationships and origin will be discussed.

***Malacothrix phaeocarpa* W. Davis, sp. nov.**—TYPE: USA, California, San Luis Obispo Co., north side of west Cuesta Ridge, along unpaved road, ca. 0.3 mi S of intersection with Tassajera Creek Rd, 1.8 mi W of U.S. 101, SE-facing slopes, in loose shale at edge of roadcut, 17 May 1990, *Davis 462* (holotype, DS; isotypes, CAS, DHL, MO, OBI, RSA, SBBG, UC, US). Careful examination of the holotypes of *Malacothrix obtusa* Bentham (K), and *M. parvifolia* Bentham (K) indicates that both are *M. floccifera*, not *M. phaeocarpa*, and that Blake (1924) was correct when he reduced *M. obtusa* to *M. floccifera*.

Herbae annuae, 5–44 cm altae e radice palari orientes. Caules superi vel e base ramosi, subglaucci, subrecti. Folia basales rosulata, oblanceolata vel obovata, subcarnosa, 2–7 cm longa, 6–20 mm lata, marginibus 3–8 paribus dentium et lobis curtis, latis subaequalibus, plerumque dentatis, acuti-vel obtuso-apiculatis et basi lobi omnis areis pilorum curtorum alborum praedita. Folia caulina infima foliis basilibus similia, sursum multum reducta, lanceolata, ovata vel oblanceolata. Folia suprema lobis basalibus, curtis, angustatis, in paribus 1–2 praedita, in $\frac{2}{3}$ areae distalis margines integros praebentia.

Capitula per anthesin 2–3.6 mm diametro, basi rotunda. Involucrum 5–8 mm, phyllariis externis plerumque viridibus, deltoideis vel lanceolatis, marginibus albis et phyllariis interioribus linearibus vel lanceolatis, acuti-apiculatis praedita. Receptaculum nudum. Flores 30–65, corollis 5.4–8.0 mm, albis et ligulis plerumque exsertis 1.5–2.5 mm praediti. Fructus 1.2–2.0 mm, brunnei vel rubro-brunnei, costis 15, distinctis acuti-apiculatis earum 5 prominentibus et pappo externo coronam scariam crenatam setis persistentibus carentem formanti praediti. $2n=14$. Auto-gonimae.

Annual, 5–44 cm from a taproot. Stems branched above or from the base, somewhat glaucous, generally erect. Basal leaves in a rosette, oblanceolate to obovate, somewhat fleshy, 2–7 cm long, 6–20 mm wide, margins with 3–8 pairs of teeth and short, broad, nearly equal, generally toothed lobes 2–7 mm with acute or blunt apices, patches of short, white hair generally at the base of each lobe. Lowest cauline leaves similar to basal leaves, greatly reduced upward, lanceolate, ovate, or oblanceolate. Uppermost leaves with 1–2 pairs of short, narrow basal lobes, the distal $\frac{2}{3}$ with entire margins. Heads 2–3.6 mm in diameter in flower, base rounded. Involucre 5–8 mm; outer phyllaries generally green, deltoid to lanceolate, margins white; inner phyllaries linear to lanceolate, with acute apices. Receptacle without bristles. Flowers 30–65; corolla 5.5–8.0 mm, white; outer ligules generally exserted 1.5–2.5 mm; fruit 1.2–2 mm, medium brown or reddish-brown, with 15 well defined ribs with acute apices, 5 prominent; outer pappus a scarious, crenate crown with no persistent bristles. $2n=14$. Self-compatible and self-pollinating.

PARATYPES. USA, California, Monterey Co., near stage road to Jolon, *Dudley s.n.* (DS 889, not DS 890); along the trail to Skinners Ridge above Boucher's Gap, *Howitt 1146* (CAS); gravelly hills, Monterey, *Parry s.n.*, Mexican Boundary Survey (K, NY); Monterey, *Torrey s.n.* (K); San Luis Obispo Co., cleared chaparral, Santa Barbara Rd, Atascadero, Santa Lucia Mts., *Hardham 4810* (CAS, SBBG, UCSB); on sandstone in burned chaparral area, Franklin Cr, Adelaida, Santa Lucia Mts., *Hardham 6915* (UCSB); burn in *Pinus attenuata* woods E of Cuesta Grade, *Hardham 9012* (UCSB); ridge SE of Cuesta Pass, disintegrating shale, *Hoover 8916* (CAS, OBI); Cuesta Ridge Botanical Area, extreme N edge along powerline road, 0.3 mi SW of intersection with Tassajera Creek Road, *Junak 4122* (DHL, SBBG); Cuesta Ridge Botanical Area, along private dirt road, ca. 1.8 mi W of Hwy 101, and 0.3 mi S of Tassajera Creek Road, *Junak 4350* (SBBG); Santa Barbara Co., near Santa Barbara, Santa Inez Mts., *T.S. Brandegees s.n.*, (UC); near summit of Harris Grade, Purisima Ridge, *Breedlove 2596* (DS, UCSB); dry slope in pine woodland, road from Figueroa Mt. to Cachuma Saddle, just N of Ranger Peak, *Chandler 3109* (SBBG); along Hwy 1, 3.2 mi S of

junction with hwy 135, above oil pumping station in grove of Bishop pine on diatomaceous soil, *Davis 455*, (DHL, SBBG); Painted Cave Ranch, *Eastwood 116* (US); gravelly slopes, Figueroa Mt., San Rafael Mts., *Hoffman s.n.* (SBBG); open gravelly flat, Figueroa Mt., *Hoffman s.n.* (SBBG); brushy slope, 5 mi N of Lompoc, *Hoffman s.n.* (SBBG); Purisima Hills, *Jepson 11957* (JEPS); Camino Cielo, between San Marcos Pass and Bush Peak, area of Refugio Pass burn of 1955, *Pollard s.n.* (CAS); on burn among Bishop pine on N side of Harris Grade, Purisima Hills, *Smith 6290* (DHL, SBBG); chaparral burn on El Camino Cielo, ca. 5.4 mi W of San Marcos Pass, *Smith 4585* (SBBG); hillside, chaparral burn along El Camino Cielo, ca. 6.2 mi W of San Marcos Pass, approximately S of Hot Springs Cyn, *Smith 4529* (SBBG); Santa Clara Co., ranch below Cattermoles, Santa Cruz Mts., Loma Prieta, *Dudley s.n.* (DS).

Malacothrix floccifera and *M. phaeocarpa* are endemic to the California Floristic Province as described by Raven and Axelrod (1978). Although *M. floccifera* is relatively widely distributed, *M. phaeocarpa* apparently is restricted to the southwestern margins of the range of *M. floccifera* (Fig. 1), and generally falls within the distribution of *M. floccifera*; however, *M. phaeocarpa* occurs in the Purisima Hills, Santa Barbara County, where *M. floccifera* apparently has not been collected. Although *M. floccifera* and *M. phaeocarpa* generally occupy similar habitats (loose soils on burns or slides) in the southern portion of the distribution of the former, no sympatric populations are known. However, *M. phaeocarpa* has been collected in chaparral within three miles of a population of *M. floccifera* in Santa Barbara County.

Found at elevations from 100–1400 m, *Malacothrix phaeocarpa* grows in openings in chaparral, but also occurs in openings in *Pinus attenuata* or *Pinus muricata* woods. The species occurs on soils derived from shale, sandstone or diatomaceous earth. Associated species in San Luis Obispo and Ventura counties include *Adenostoma fasciculatum*, *Arctostaphylos glandulosa* ssp. *glandulosa*, *Calandrinia breweri*, *Cryptantha clevelandii*, *Dendromecon rigida*, *Emmenanthe penduliflora*, *Eriogonum cithariforme*, *Erodium cicutarium*, *Eschscholzia caespitosa*, *Hypochoeris glabra*, *Lactuca serriola*, *Lotus junceus*, *Lotus salsuginosus*, *Pinus attenuata*, *Pinus muricata*, *Pseudotsuga menziesii*, *Quercus durata*, *Quercus wislizenii*, *Senecio vulgaris*, and *Silene multinervia*.

Populations of *M. floccifera* are associated with a number of plant communities including chaparral, juniper-digger pine woods, oak woodlands, redwood forests, transition forests, and yellow pine forests. The species grows on serpentine soils, loose clay soils, gravelly soils, or fine sand at elevations from 100–2100 m. Associated species in San Luis Obispo and Santa Barbara counties include *Adenostoma fasciculatum*, *Artemesia tridentata*, *Calystegia fulcrata* ssp. *mala-*



FIG. 1. Distribution of *Malacothrix floccifera*, and populations of *M. phaeocarpa* in California.

cophylla, *Dendromecon ridiga*, *Emmenanthe penduliflora*, *Eriogonum fasciculatum*, *Galium andrewsii*, *Langloisia schottii*, *Lotus sal-suginosus*, *Phacelia cicutaria*, *Quercus douglasii*, *Rhus trilobata*, and *Salvia columbariae*. In the western portion of its distribution, *M. floccifera* parallels the distribution of chaparral in the California Floristic Province in the Transverse Ranges in Ventura County, and northward in the Coast Ranges. In the eastern portion of its distribution *M. floccifera* follows the distribution of chaparral in the Sierra Nevada north of Madera County (Fig. 1), but is associated with other plant communities at higher elevation.

On the basis of growth habit, leaf morphology, leaf hair distribution, involucre length, involucre morphology, and fruit size *Malacothrix phaeocarpa* and *M. floccifera* are not consistently distin-

TABLE 1. A COMPARISON OF *MALACOTHRIX FLOCCIFERA* AND *M. PHAEOCARPA* GROWING TOGETHER IN A GROWTH CHAMBER.

	<i>M. floccifera</i>	<i>M. phaeocarpa</i>
Involucre height (mm)	4.2-9.0	5.1-8.0
Number of involucre bracts	16-30	15-19
Width of flower heads in flower (mm)	2.7-4.2	2.2-4.5
Number of florets in a head	19-63	21-66
Corolla length (mm)	7.2-15.1	5.4-8.0
Ligule length (mm)	5.0-10.0	2.1-4.2
Ligule width (mm)	2.7-4.2	1.0-1.7
Outer ligule exertion (mm)	5.4-9.0	1.5-2.5
Length of receptacle bristles (mm)	2.3-3.0	none
Stamen length (mm)	5.5-7.0	3.5-5.4
Distance, tip of anther to base of style branches (mm)	1.2-4.1	0.2-1.5
Achene length (mm)	1.3-2.1	1.4-2.0
Length of inner pappus (mm)	3.2-5.8	3.6-4.3
Growth rate after bolting (mm/day)	1.5-3.2	3.4-4.6

guishable (Table 1). The two species differ, however, in several floral features. In *M. floccifera* ligules are well-exserted beyond the involucre; the receptacle has thin, smooth, somewhat fragile bristles as long as 4 mm; there is no outer pappus on achenes; and, apices of intermediate achene ribs between pairs of strong ribs are flattened. In *M. phaeocarpa* ligules extend less than 3 mm beyond the involucre; the receptacle is without bristles; a scarious, crenate outer pappus is present at the achene apex; and, the intermediate ribs of the achene are well-defined. Ligules of *M. phaeocarpa* are white to cream-white, and bear an abaxial purplish stripe. Ligules of *M. floccifera* are generally white with an abaxial purplish stripe, but populations of yellow-flowered plants occur in the western area of distribution, and are indistinguishable from white-flowered plants in features other than flower color. In several populations of *M. floccifera* along the road through Rose Valley, Ventura County, there is found a continuum of corolla color shades ranging from white to yellow.

Achenes of *Malacothrix phaeocarpa* are dichromic. In progenies in growth chamber culture 17% of the achenes were reddish-brown, and were found in the distal rows of mature flower heads. The rest of the achenes were light to medium brown, and generally were found in the inner portion of the flower head. Achenes of *M. floccifera* are grey, brown, or purple-brown; in a majority of them a dark line is visible through the fruit coat in the middle portion of the achene. The source of the line is a narrow ring of black pigment circling the embryo just below the base of the cotyledons. In cross-section, the interior tissue of the embryo is white; the black pigment occurs only in the outer cells.

RESULTS OF GROWTH CHAMBER STUDIES

Representatives of two populations of *M. phaeocarpa* in Santa Barbara County (Breedlove 2596, SBBG; Davis 445, DHL, SBBG) and one population in San Luis Obispo County (Junak 4122, SBBG, DHL) were grown in growth chambers at the University of Louisville (see Davis and Philbrick 1986 for a description of general methods). Propagated at the same time were representatives of four populations of *M. floccifera*, two in Placer County (Baad 4757, MCAF; Baad 3403, MCAF) and two in Ventura County (Davis 401, DHL; Junak 3046, DHL, SBBG). Less than 10% of the achenes of either species germinated in petri dishes; achene tips were punctured with a needle to increase germination rate. In general, plants of *M. phaeocarpa* bolted, flowered, and commenced senescence sooner than plants of *M. floccifera* growing alongside them. In addition, heads of *M. phaeocarpa* were noticeably less nodding in bud than heads of *M. floccifera*. Meiotic chromosome counts of $2n=7_{II}$, and root tip mitotic counts of $2n=14$ were obtained for both species; pollen stainability in plants grown from wild achenes was 90–100%.

All *M. floccifera* grown from wild achenes (30 plants), and from intra-populational crosses (34 plants), was self-incompatible. However, eight of 15 plants from intraspecific crosses between representatives of a Placer County population and representatives of a Ventura County population were self-compatible; none of these plants had any of the morphological diagnostic features of *M. phaeocarpa*.

All *M. phaeocarpa* grown from wild achenes (26 plants), or from achenes from self- or sister-pollinations (35 plants) was self-compatible and self-pollinating.

Artificial interspecific hybrids between *Malacothrix floccifera* and *M. phaeocarpa* were difficult to produce; only 15 filled achenes were produced from 115 cross-pollinations involving *M. floccifera* as the female parent. Eight achenes germinated and produced mature plants; 1 plant was male sterile and a product of self-fertilization via the mentor effect (Davis 1984), and seven plants were hybrids with stainable pollen of 0–10%. One hybrid was produced from crosses involving *M. phaeocarpa* as the female parent; it had 3% stainable pollen. Chromosome pairing was variable in hybrids and the maximum chromosome association was 2 pairs, six univalents, and a chain of four.

THE ORIGIN OF MALACOTHRIX PHAEOCARPA

Of all of the extant species of *Malacothrix*, *M. floccifera* is the one most similar to *M. phaeocarpa* in a majority of features including growth habit, details of vegetative morphology, involucre morphology, and habitat preference. Breeding system differences support

the hypothesis that the relationship between *M. floccifera* and *M. phaeocarpa* is a progenitor-derivative one. Some of the floral differences between the allogamous *M. floccifera* and the autogamous *M. phaeocarpa* are of the sort that have been found to be associated with the evolution of autogamy in other groups of plants (Wyatt 1988). These include differences in corolla length, in degree of exertion of ligules, in ligule width, in anther length, and in distance from anther tip to base of style branches (Table 1). Other differences, however, such as presence of numerous, long receptacle bristles in *M. floccifera* (none in *M. phaeocarpa*), a well-developed outer pappus in *M. phaeocarpa* (absent in *M. floccifera*), well-defined intermediate ribs of achenes of *M. phaeocarpa* (flattened in *M. floccifera*), and differences in chromosome structure are not generally correlated with a shift in breeding system, and suggest that the origin of *M. phaeocarpa* may have involved a multistep process of selection over an extended period of time.

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